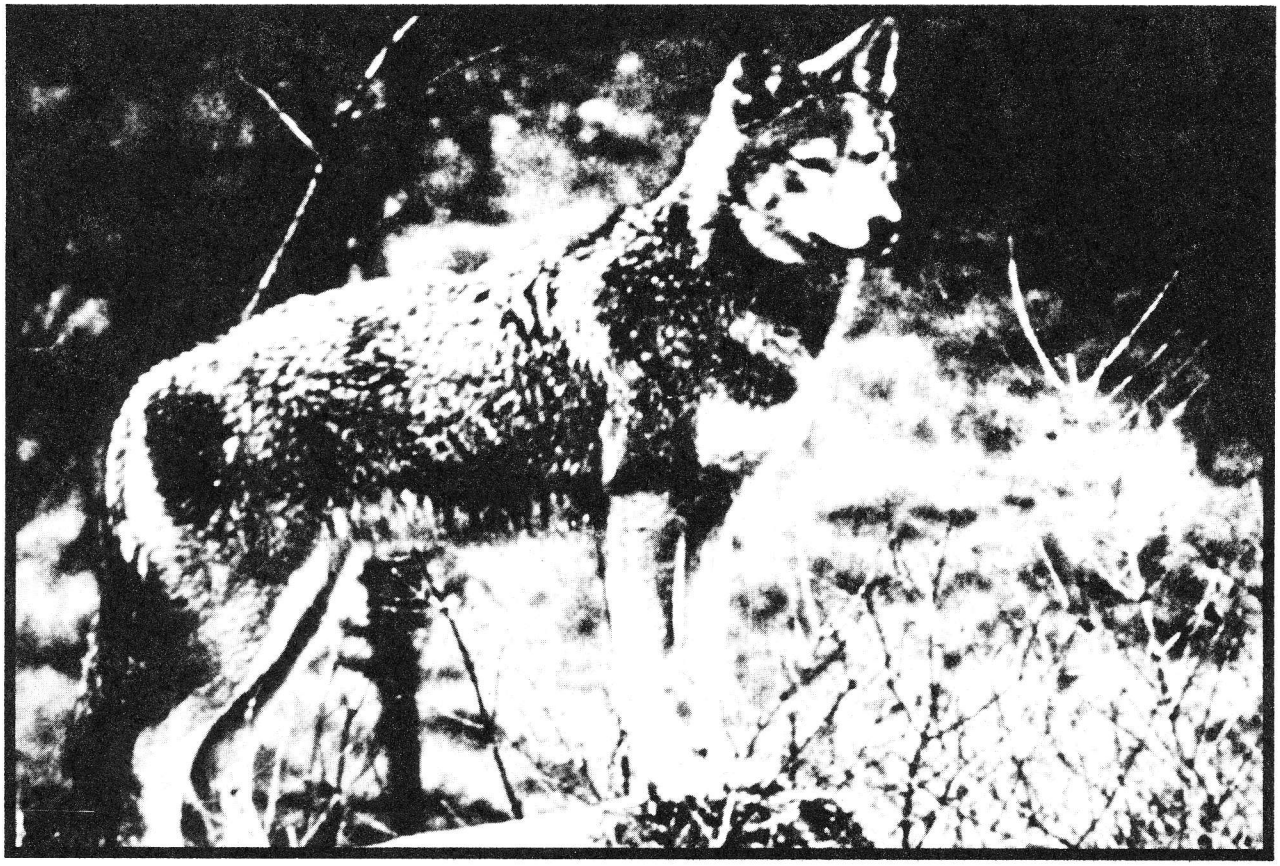
RED WOLF MANAGEMENT SERIES
TECHNICAL REPORT NO. 5

RED WOLF TAXONOMY
A REVIEW



U.S. FISH AND WILDLIFE SERVICE
SOUTHEAST REGION
ATLANTA, GEORGIA

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TECHNICAL REPORT NO. 5

RED WOLF TAXONOMY

A REVIEW

BY

WARREN T. PARKER
U.S. FISH AND WILDLIFE SERVICE
100 OTIS STREET, ROOM 224
ASHEVILLE, NORTH CAROLINA 28801

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Introduction

The science of taxonomy involves classifying living organisms and determining their relationships with one another. Classical taxonomy has traditionally been a "hands-on" science, concerning itself with morphological characteristics in typically small samples of individuals collected from a much larger population. Only recently have scientists begun to understand those individuals that comprise a species as the dynamic, living population which they are or once were. The mammalian genus Canis has been noted for many years for problems regarding definitions of taxonomic classification. Many investigators have been frustrated because chromosome number and structure are constant throughout the genus (Atkins and Dillon 1971). In addition, species and subspecies of this genus can interbreed, producing viable hybrids. This report is prepared to provide an updated assessment of the more significant literature that discusses the taxonomy of the red wolf (Canis rufus).

The red wolf is an endangered taxon that is a classic example of a segment of our wild heritage that declined to the point of needing extraordinary help in order to save it from extinction. The taxonomic issue also runs prominently through the story of the red wolf. Our knowledge of this species before it came dangerously close to extinction is marginal at best. The literature prior to World War II contains few factual references to these uniquely southern animals. Much of what we do know is traced to those few surviving animals that were found in southern Louisiana and Texas.

There are two major taxonomic problems involving C. rufus. The first is whether the red wolf, as it originally existed, was a distinct species of wolf or only a subspecies of one of the other two kinds of Canis in North America--the gray wolf (C. lupus) or the coyote (C. latrans). The second systematic problem concerns what happened to the wild canid population of the Southeast during the first half of the present century. This report addresses only the first issue. The second issue is thoroughly discussed by Paradiso and Nowak (1971) and Nowak (1979).

History

Before the twentieth century, the canids of the Southeast had been assigned various scientific and common names, primarily by people who had not closely studied the animals. Among these early naturalists was Bartram (1791), who first described the red wolf in Florida. Writings dating back over 300 years mention wolves throughout the Southeastern United States, from central Texas to Florida and north to the Ohio River Valley. Audubon and Bachman, in their classic work (1851), were the first to suggest that in the southern states there existed a wolf that was structurally different from other wolves they had seen. They described the "Black American Wolf" as occurring only in Florida, South Carolina, North Carolina, Kentucky, southern Indiana, southern Missouri, Louisiana, and northern Texas. They also discussed the "Red Texan Wolf," which they thought ranged from northern Arkansas through Texas and into Mexico, but believed all the wolves they described were only varieties of one species. The coyote

(Canis latrans) was described as a full species, uniquely different from the wolves of North America.

Unfortunately, the red wolf was exterminated from most of its range by the early part of this century (Nowak 1972). Few specimens were preserved, and there were no definitive descriptions of the animal's appearance or life history. Because of this, we know little of the animal under natural conditions. During the late 1800s and early 1900s some significant revisions were initiated in the taxonomy of this unique wolf. Bangs (1898) determined that the Florida wolf should be elevated to full species level (Canis ater), while Bailey (1905) elevated Audubon and Bachman's "Red Texan Wolf" to a full species with the name Canis rufus. Bailey assigned this new species to a range in southern and central Texas. Vernon Bailey was the chief field naturalist of the U.S. Biological Survey (predecessor of the U.S. Fish and Wildlife Service) and was the first knowledgeable biologist to examine the wild canids of Texas. He found the small red wolf of the south-central part of the state to differ so greatly from the larger gray wolf of the plains just to the west that the two deserved to be treated as completely different species. Miller (1912) designated the Florida wolf as Canis floridanus, which generally became accepted for all wolves in the forested areas of the Southeastern United States, while C. rufus continued to be recognized in central and southern Texas (Nowak 1979).

Years later, Edward A. Goldman (Goldman 1944), senior biologist with the Biological Survey, examined a larger number of canid specimens and found

that the Texas red wolf intergraded in characteristics with the canids across the Southeastern United States to Florida, including a continuity of key cranial and dental features. Goldman thus consigned all of the wolves of the Southeast to one species, C. rufus. By the time of the publication of this revisionary work in 1944, the red wolf had already been extirpated east of the Mississippi River. Goldman listed C. r. rufus for the small Texas subspecies; C. r. floridanus for the eastern subspecies; and C. r. gregoryi, a new subspecies in the lower Mississippi Valley. Goldman's nomenclature persists to the present time for the red wolf (see Figure 1).

Later investigators have generally supported Goldman's classification. An exception to this occurred when Lawrence and Bossert (1967), two biologists at Harvard University, performed a multiple character analysis of North American Canis. This study involved carefully making a set of measurements on a series of skulls and then subjecting the resulting figures to numerical analysis by computer. It was hoped that the computer analysis would show how the different types of specimens were related to each other. The skulls examined included those of 20 gray wolves, 20 coyotes, 20 domestic dogs (C. familiaris), and a small number of red wolves collected before 1920. The results of their study suggested that the red wolf was close enough to the gray wolf to be considered only a subspecies of the latter (Nowak 1970).

Paradiso (1968) and Nowak (1979) suggested that Lawrence and Bossert's sample size had been too small and did not truly represent the great

Fig. 1. Map showing localities of C. rufus from archeological sites (triangles), and fossil C. rufus (black dots). The solid lines show the distribution of subspecies: C. rufus rufus (R), C. rufus gregoryi (G), and C. rufus floridanus (F). Because of scale of map, it is not possble to plot all localities in crowded areas. (From NOWAK: 1979).

geographic and individual variation of the canids. Paradiso and Nowak (1971) also discussed the issue in the U.S. Fish and Wildlife Service publication, Special Scientific Report - Wildlife No. 145: A Report on the Taxonomic Status and Distribution of the Red Wolf, in which the demise of the red wolf in Texas and hybridization problems between the red wolf and the coyote were documented. A large sampling of skulls of C. rufus, C. lupus, and C. latrans was also analyzed, and a determination was made that the red wolf is a distinct species.

Later, Nowak (1979), in examining the systematic problems in the genus Canis in North America, conducted multivariate analyses on approximately 5,000 canid skulls. His conclusions, as well as those of Kurten and Anderson (1980), agree in the probable derivation of the red wolf from a coyote-wolf ancestor and a later separation of the gray wolf, which entered (or reentered) North America at a later date. Nowak (1979:87) expressed his conclusion as follows:

> "In nearly all measurements and other features in which C. rufus differs from C. lupus, the former approaches C. latrans. Indeed, available specimens of the red wolf almost bridge the morphological gap between the proximal extremes of the other two species. Hybrid origin for C. rufus thus seems to be one possibility, but there are other solutions to the problem. The most reasonable explanation is that C. rufus represents a primitive line of wolves that has undergone less change than

> C. lupus, and has retained more characters found in the ancestral stock from which both wolves and coyotes arose."

In later assessing these conclusions, Nowak (1989) reaffirms his position:

> "That last particular statement reflects one of the positions in my dissertation about which I feel most confident. The original characters of C. rufus can be traced back long before hybridization would have begun, even into the Pleistocene. C. rufus did not have a hybrid origin, but it does retain ancestral features, and thus it is morphologically shifted away from C. lupus in the direction of C. latrans."

It is significant to note that Nowak continued his line of thought by commenting that his above-referenced conclusion:

> "...does not necessarily mean that C. rufus is a distinct species. One could argue that, while C. rufus is primitive, C. lupus never became completely isolated from it genetically, and that the two were blending to some extent where their ranges met in North America. Unfortunately, there are very few specimens from appropriate times and places. My own samples showed so little overlap that I considered it best to treat the two as distinct species."

In a comparative gross morphological study of the cerebellum in six species of the genus Canis, Atkins and Dillon (1971) confirmed the distinct speciation of C. rufus and concluded that while the red wolf is most closely related to C. lupus in its cerebellar features, it appeared to be more primitive in several aspects than any of the other species of Canis considered. A related study of canids from Missouri by Elder and Hayden (1977) demonstrated, by multivariate analysis of skulls collected, a complete separation of coyote, dog, gray wolf, and red wolf. This investigation also determined that during the 1940s and 1950s there was an infusion of red wolf genes into the coyote population as the red wolf was being exterminated in Missouri. This information reinforces conclusions reached later by Nowak (1979) and other researchers.

In an unpublished letter dated December 7, 1981, Dr. Donald C. Morizot (copy attached), a researcher at the University of Texas System Cancer Center, wrote to Service biologist Curtis J. Carley regarding his biochemical-genetic study of the evolution of canid species. He stressed the fact that few biochemical-genetic differences among living Canis species have been discovered. Dr. Morizot's study, however, did detect "substantial genetic variation at three enzyme loci" in red blood cell samples in comparisons of dogs, coyotes, red wolves, and gray wolves. Samples of red wolf blood cells examined resulted in an allele not seen in any other Canis. He concluded that the red wolf is genetically more similar to the coyote than to the gray wolf but possesses an allele unknown in coyotes. Additional data derived from skull measurements of red wolves and coyotes in early collections convinced him of the integrity of the red

wolf as a separate form which should be recognized as a small wolf which evolved in North America.

On the other hand, after Lawrence and Bossert (1967) published their contention that the red wolf should be treated as a subspecies of the gray wolf, other investigators have supported their findings, including Mech (1970) and Clutton-Brock (1989). It is interesting to note that the literature is not consistent in the ancestral relationship of C. rufus in the genus Canis, even among those investigators who support speciation. While Lawrence and Bossert (1967) and Atkins and Dillon (1971) differ on the question of speciation, both consider the red wolf to be closely allied to C. lupus. Conversely, both Nowak (1979) and Morizot (1981) support speciation but consider the red wolf to be more closely related to C. latrans.

At the time of this writing, efforts are underway to critically assess biochemical variations within the wild canids of the United States utilizing the latest techniques in analyzing blood chemistry and DNA. Red wolf blood samples have recently been furnished several researchers. It will probably be a year or more before definitive information is available to either support or reject the issue of speciation based on these tests. It should be noted, however, that all factors, including morphological and others, will have to be weighed in making any determination of speciation. No one single test can be relied on in addressing this important concern.

In the interim the words of Clutton-Brock (1989) serve to guide red wolf recovery efforts:

> "I very much hope that you will be successful in your efforts to conserve the red wolf, which (whether it is called a race of Canis lupus or a distinct species of wolf) is clearly a distinctive wild canid that is in severe danger of extinction and whose demise would mean a severe loss of biological diversity within the dwindling group of large carnivores."

The U.S. Fish and Wildlife Service recognized the red wolf as a species in its listing as an endangered species in 1967 (32 FR 4001). Subsequent Federal Register notices regarding the red wolf include 1979 (44 FR 29571) and 1980 (45 FR 33768-33781).

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The University of Texas System Cancer Center

Science Park 389
P.O. Drawer XXX • Smithville, Texas 78957

512/237-2403

Research Division

December 7, 1981

Mr. Curtis Carley
U.S. Department of the Interior
Fish and Wildlife Service
P.O. Box 1306
Albuquerque, New Mexico 87103

Dear Curt:

Thanks for your request for additional information concerning the significance of our biochemical genetics research in furthering the understanding of the evolution of canid species. I will try to keep my comments brief but adequate to explain the current state of the art.

First, it should be pointed out that few biochemical genetic differences among living Canis species have been discovered. Vibeke Simonsen from Denmark expressed her concern to us that perhaps her electrophoresis system was at fault when she failed to find major differences between gray wolves and domestic dogs. The fact is that carnivores, in general, exhibit very low levels of heterozygosity; numerous laboratories have confirmed this conclusion. All electrophoretic studies of Canis species, in particular, have agreed in finding low average heterozygosity and few differences among domestic dog breeds and wild members of the genus. Such a result implies either a recent evolutionary divergence or a population structure which minimizes heterozygosity and possibly genetic divergence through fixation of new allelic mutations. Of course, these possibilities are not mutually exclusive.

We are faced, then, with attempting to assess the evolutionary relatedness of genetically very similar species, whatever the reason for the strong similarity. The data collected by Bob Ferrell and I concerning electrophoretic variation must be interpreted with such a similarity in mind. We have analyzed red blood cell samples from over 400 domestic dogs of a wide variety of breeds, and have compared those results to our data from the largest sample of coyotes and red wolf-range animals yet analyzed. We have detected substantial genetic variation at three enzyme loci which I would like to discuss here: LDH-A, GPI, and GOT-S. The first salient point to be emphasized is that, despite stringent inbreeding and large scale morphological differentiation, domestic dogs exhibit no variability at LDH-A and only very rare variants at GPI and GOT-S. In contrast, coyotes from three geographically distant areas in Texas exhibit considerable variability at GPI and GOT-S, but not at LDH-A. Canis rufus-range wild canids possess variability at all three loci.

Turning to studies of gray wolves (Canis lupus), no variability has been demonstrated at any of these three loci. In fact, the gray wolf genetically is identical to all but a few (< 1%) domestic dogs with respect to these genes. No more than 10% of coyotes or red wolf-range wild canids, on the other hand, are identical to domestic dogs or gray wolves in our studies. I must feel that coyotes and red wolf-range animals are genetically distinct from gray wolves and dogs. Almost all mammalogists agree, at least with respect to coyotes. I am aware of no authority who assigns gray wolves and coyotes to the same species.

Such a conclusion leads one to examine the relationships of the red wolf as it is represented by individuals in southeast Texas and southwest Louisiana remnant populations. Is it a coyote? Is it a small gray wolf form? Is it a gray wolf-coyote hybrid? I can state with some certainty that it is more like a coyote than like a gray wolf or a dog. At GPI and GOT-S, it shares alleles with coyotes which are found rarely in dogs, and, to our present knowledge, never in gray wolves. But at the LDH-A locus, red wolf-range animals possess an allele not seen in any other Canis. The frequency of this allele is in inverse proportion geographically to the presumed extent of coyote hybridization with the remaining red wolves: a west-to-east cline in the "red wolf LDH-A" allele is observed from Brazoria County, Texas to Cameron Parish, Louisiana. What the level of genetic difference was between red wolves and coyotes before coyote range extension is impossible to determine at this late date. What is reasonably certain is that an allele known only in red wolves has been identified.

How does such an interpretation of Canis relationships fit with the fossil record? The evolutionary schemes of Nowak and of Kurten and Anderson both agree in the probable derivation of the red wolf from a coyote-red wolf ancestor and a more distant separation from the gray wolf, which entered (or re-entered) North America at a later date. Gene frequency data at the three polymorphic loci discussed here agree with such an interpretation. With the exception of the LDH-A variant which appears to be unique to red wolves, alleles at each of the three loci are shared by gray wolves, coyotes, and red wolves. The gray wolf allele for GOT-S is common in coyotes and red wolves, but a second allele not known from gray wolves is shared by the latter. At GPI, the gray wolf allele is found in coyotes and red wolves, but is rare relative to a second allele in the latter two species. I conclude that the red wolf is genetically more similar to the coyote than to the gray wolf, but possesses an allele unknown at present in coyotes. Additional data derived from skull measurements of red wolves and coyotes in early collections have convinced me of the integrity of the red wolf as a separate form which should be recognized as a small wolf which evolved in North America. Such a conclusion well fits all the available data, both from biochemical genetic studies and from the fossil record.

I should conclude by noting that other biochemical differences among Canis species do exist, and I have observed several variants possibly useful in determining red wolf ancestry in animals utilized in captive breeding progrms. Studies such as those I have described cannot be conducted without money for supplies. I would like to take this opportunity to state that the lack of federal commitment in funding the efforts to preserve the red wolf, particularly with regard to necessary basic research, may well mean the demise of a species once unique to American forest lands.

With best regards.

Sincerely,

Donald C. Morizot

Donald C. Morizot, Ph.D.
Research Associate

DCM:pgm